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Interannual and Spatial Feeding Patterns of Hatchery and Wild Juvenile Pink Salmon in the Gulf of Alaska in Years of Low and High Survival

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Abstract.—To improve understanding of the mechanisms affecting growth and survival, we evaluated the summer diets and feeding patterns (prey composition, energy density, and stomach fullness) of hatchery and wild juvenile pink salmon *Oncorhynchus gorbuscha* in Prince William Sound (PWS) and the northern coastal Gulf of Alaska (CGOA). Our study (1999–2004) included 2 years of low (~3%), mid (~5%), and high (~8–9%) survival of PWS hatchery pink salmon. Because variations in diet should affect growth and ultimately survival, we expected that the variations in diet, growth, and survival would be correlated. During August in the CGOA, pteropod-dominated diets and higher gut fullness corresponded to high survival (5–9%), and copepod-dominated diets and lower gut fullness corresponded to low survival (3%). Within years, no significant differences were found in diet composition or gut fullness between hatchery and wild fish or among the four PWS hatchery stocks. Diets varied by water mass (habitat) as juveniles moved from PWS to more saline habitats in the CGOA. In July, when juveniles were most abundant in PWS, their diets were dominated by pteropods and hyperiid amphipods. The diets of fish that moved to inner-shelf (i.e., the least-saline) habitat in the CGOA in July were dominated by larvaceans in low-survival years and pteropods in high-survival years. Diet quality was higher in CGOA habitats than in PWS in July. In August, fish moved to the more productive, more saline water masses in the CGOA, where large copepods and pteropods were dominant prey and diet quality was better than in PWS. Our results indicate that spatial variation in the diets of juvenile pink salmon in July and the timing of migration to the CGOA play a critical role in marine growth and survival.

The Northeast Pacific Global Ocean Ecosystems Dynamics (NEP–GLOBEC) Program was designed to investigate how two continental shelf ecosystems, the California Current System and the coastal Gulf of Alaska (CGOA), respond to large-scale climate change (U.S. GLOBEC 1996; Weingartner et al. 2002). One core hypothesis of NEP–GLOBEC is that ocean survival of Pacific salmon *Oncorhynchus* spp. is primarily determined by survival of juveniles in coastal regions, and is affected by interannual and interdecadal changes in physical forcing and by changes in food web dynamics. Pink salmon *O. gorbuscha* were selected as the target species to address this hypothesis

in the CGOA shelf ecosystem because they are highly abundant zooplanktivores that spend little or no time rearing in freshwater as juveniles and support valuable commercial fisheries as adults (Clark et al. 2006). In addition, they have a shorter lifespan (2 years) than other Pacific salmon species, which provides a more direct link between short-term climatic change and forcing mechanisms that drive marine food web dynamics.

Numerous studies reviewed by Ruggerone and Nielsen (2004) have documented that pink salmon seem to have a competitive advantage over other salmonid species in the North Pacific Ocean owing to their high abundance, high consumption rates, rapid growth, and ability to use a wide variety of prey species, including those of lower trophic levels. Run strength of pink salmon is thought to be determined

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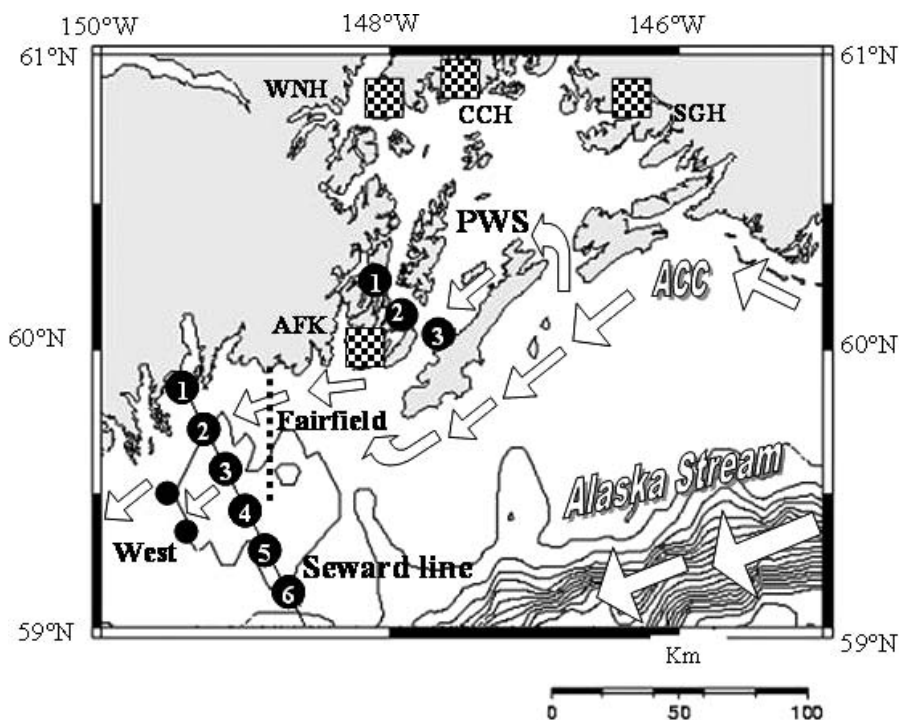


FIGURE 1.—Prince William Sound (PWS) and Gulf of Alaska sample sites, including the Cape Fairfield Line, Seward Line (sites 1–6), and two West stations. The locations of the Armin F. Koenig (AFK), Cannery Creek (CCH), Solomon Gulch (SGH), and Wally Noerenberg (WNH) hatcheries within PWS are indicated, as are the relative locations and directions of the nearshore Alaska Coastal Current (ACC) and the Alaska Stream.

during their early marine life history, and can be affected by diet and availability of their zooplanktonic prey (Healey 1991; Parker 1996). Fish hatcheries release approximately 600 million juvenile pink salmon into the waters of Prince William Sound (PWS) annually during late April and May, where they mix with wild fish and reside for 3–4 months before moving into the shelf environment of the CGOA (Cooney 1993). The majority of juvenile mortality is believed to occur in late spring during inshore residence in PWS and transition to CGOA shelf waters (Parker 1968; Willette 2001), and a second significant phase of size-selective mortality occurs after the first summer (Moss et al. 2005; Cross et al. 2008).

During the sampling years of our GLOBEC project (1999–2004), marine survival rates for PWS hatchery pink salmon varied by two- to three-fold. Survival rates were low (about 3%) in 2001 and 2003, intermediate (5–6%) during 1999 and 2000, and high (8–9%) during 2002 and 2004 (ADFG 2005; PWSAC 2005). While the number of fry released during 1999–2004 ranged from a low of 586 million in 2000 to a high of 639 million in 2004, there was no direct correlation

between total hatchery releases and marine survival (L. Haldorson, unpublished data).

Weingartner et al. (2002) reviewed information on the geomorphology, oceanography, and interannual variability in the CGOA shelf ecosystem. The entire region is dominated by high precipitation and low-nutrient freshwater runoff from the coastal mountain range (PICES 2004). The northern CGOA shelf near Seward, Alaska, where most NEP–GLOBEC sampling for pink salmon occurred, can be roughly organized by salinity fronts into three distinct habitats or coastal water masses (Weingartner et al. 2002): an inner-shelf habitat dominated by low-salinity, nutrient-poor waters of the Alaska Coastal Current (ACC); a midshelf transition habitat (Front) characterized by water of intermediate salinity and highly variable flow; and an outer-shelf habitat, including the continental shelf break and inner slope (Trans), containing the more saline and nutrient-rich waters of the Alaskan Stream. Juvenile pink salmon in the northern CGOA are distributed across the continental shelf in surface waters where they feed visually on prey during daylight hours in the neuston and upper 10–20 m of the water column (Armstrong et al. 2005).

Our study extends the previous diet information from 1998 (Boldt and Haldorson 2003) and 1999–2001 (Armstrong et al. 2005). For the first time, diets of hatchery and wild juvenile pink salmon in the CGOA are compared to determine whether they reflect different feeding behaviors. Interannual and monthly variation in diets are evaluated to reflect stage-specific feeding from estuarine to coastal marine shelf habitats. Previous research found that in July, fish were significantly larger in PWS and the CGOA in high-survival years than in low-survival years, and linked faster growth of juvenile pink salmon during August in the CGOA to better marine survival at subsequent life stages. Because the growth and survival of juvenile pink salmon differ markedly among years (Cross et al. 2008) and size-selective mortality gives a survival advantage to the largest, fastest growing juvenile fish (Moss et al. 2005), we also compared the diets of small fish (three lowest quartiles) to the diets of large fish (fourth quartile) by year as well as the diets of large juvenile pink salmon during high- and low-survival years. Our results are being incorporated into on-going efforts to model the bioenergetic demands, growth, and survival of juvenile pink salmon from PWS under changing climatic conditions (Beauchamp et al. 2007a).

Methods

Field sampling.—GLOBEC field sampling was conducted at six CGOA stations (GAK 1–6) along the Seward Line in August from 1999 through 2004 (Figure 1). In 2001–2004, samples were also collected in July, September, and October at the same six CGOA stations and three stations in PWS (PWS 1–3; Figure 1). In September 2003 and 2004, additional sites on either side of the Seward Line were sampled (Cape Fairfield to the east and West Line) to follow the path of out-migrating juvenile pink salmon. All sampling in 1999 and 2001–2004 was conducted with a Nordic 264 surface rope trawl (198 m long, 25 m wide, and 35 m high [vertical height], with a 1.2-cm mesh liner in the cod end). The trawl was towed at the surface for approximately 30 min at 3.25–6.5 km/h (about 1.5–3 knots). During August 2000, fish were collected using surface gill nets (200 m long and 3 m high composed of four different 50-m panels with 19-, 25-, 32-, and 38-mm stretched mesh) deployed for an average soak time of 3 h (range, 2.5–3.8 h). Fish were taken from the net, identified to species, measured, and frozen for laboratory analyses.

Laboratory analyses.—In the laboratory all fish were thawed, weighed (g), and measured for fork length (FL) (mm). Otoliths were taken to determine hatchery of origin. A random sample of up to 15 fish

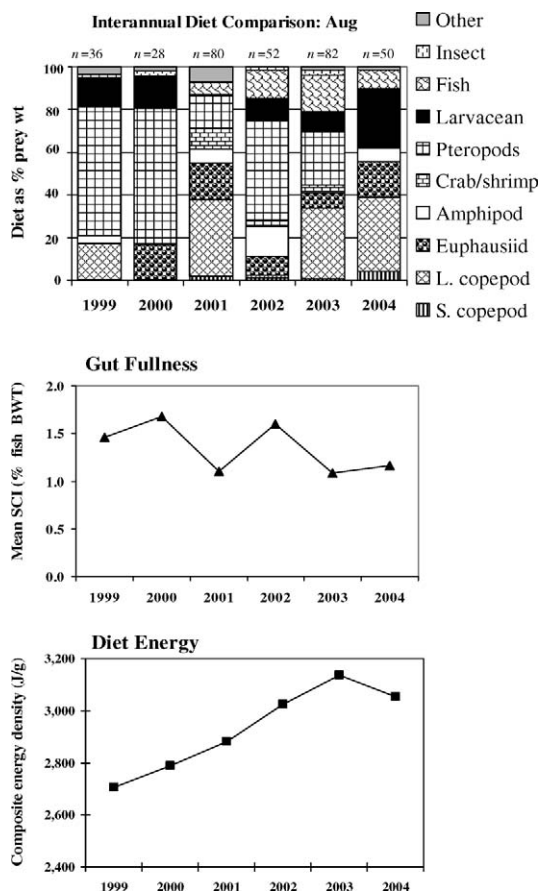


FIGURE 2.—Comparison of juvenile pink salmon diets for all Seward Line stations, August 1999–2004. The top panel shows the average prey composition by percent weight (L. = large, S. = small), the middle panel the stomach content index (SCI [see text]) as a percentage of fish body weight (BWT), and the bottom panel the composite energy density of the different diets.

from each station was designated for diet analysis. Fish sampled only during daylight hours were included in these analyses, because Armstrong et al. (2005) determined that juvenile pink salmon fed only during daylight. Stomachs were removed and contents weighed. Stomach contents were preserved in 10% buffered formalin and later transferred to 70% isopropanol. Otoliths were later examined to determine the natal origins of all fish. In the hatcheries, fish had previously been exposed to thermal shocks that left discernable marks on the otoliths, thereby identifying the particular hatchery of origin and time of release. Four hatcheries in PWS: Armin F. Koenig (AFK), Cannery Creek (CCH), Solomon Gulch (SGH), and Wally Noerenberg (WNH), participated in this program

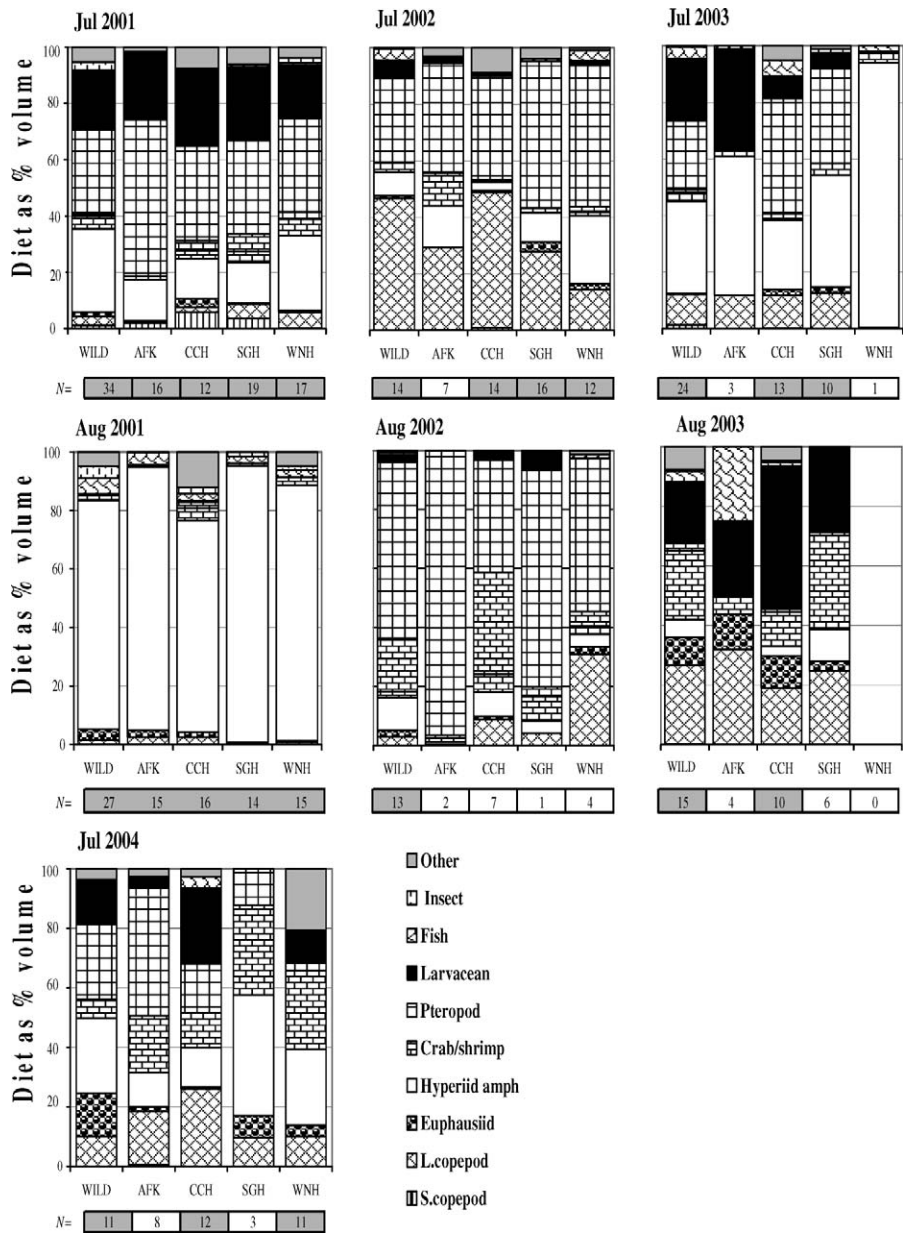


FIGURE 3.—Average prey composition of juvenile pink salmon in (a) Prince William Sound in July 2001–2004 and August 2001–2003 and (b) along the Seward Line (GAK) and Cape Fairfield Line (CF) in July and August 2002–2004 by natal source (wild versus the four hatcheries). Sample sizes are given in the boxes below the bars. Analysis of variance results were compared for groups of 10 fish or more (shaded boxes). No comparisons were possible in August 2004 because fish dispersed from Prince William Sound.

of marking juvenile pink salmon. Unmarked fish were assumed to be of wild origin, although there was a slight chance they could be from hatcheries to the south that did not mark their releases (Moss et al. 2005).

Stomach content processing followed the procedures

outlined in Armstrong et al. (2005). Stomach contents were washed onto a 63- μ m screen, then transferred to a petri dish, which was placed over an acetate sheet impregnated with a grid (squares 3.7 mm on a side), and then viewed under a dissecting microscope. The

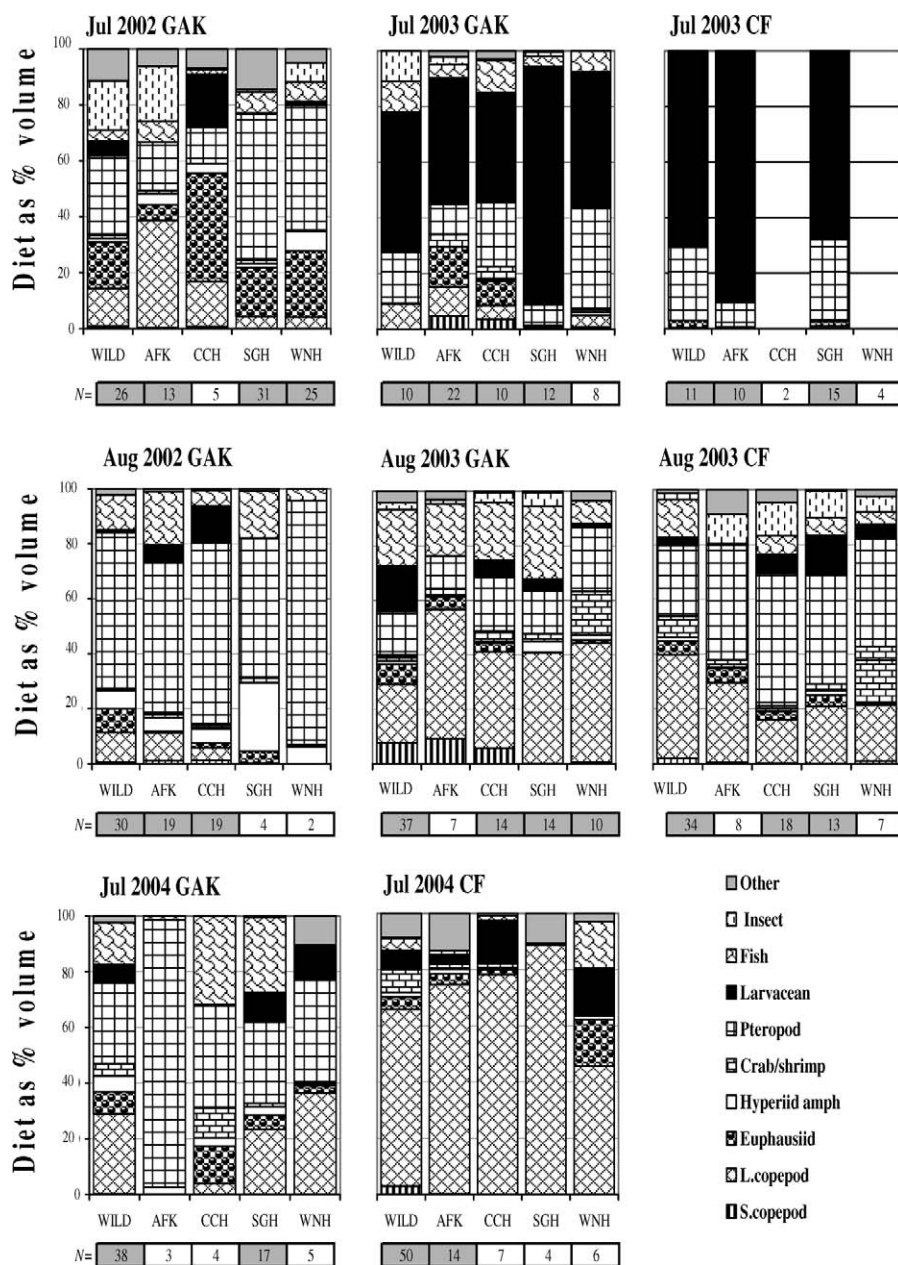


FIGURE 3.—Continued.

sample was sorted into major prey groups. Prey were identified to the lowest possible taxon and grouped into the following categories: small copepods (<2.5 mm TL), large copepods (≥2.5 mm TL), euphausiids, hyperiid and gammarid amphipods, larval crabs and shrimp, pteropods, larvaceans, larval and juvenile fish, insects, and other. The two size-groups of copepods

represented two different species assemblages identified by Coyle and Pinchuk (2003). The category “other” included any of the following prey items: barnacles (nauplii and cyprids), bivalves (veligers), cladocerans, chaetognaths, cumaceans, small gastropods, gastropod eggs, polychaetes, and juvenile squid.

Each prey category was blotted dry and spread

TABLE 1.—Diet composition (% volume) of juvenile pink salmon and ANOVA results by fish size (small [first to third quartiles] versus large [fourth quartile]) and year (2001–2004) by month (July, August) and area. The abbreviation ns stands for not significant. No pink salmon were found in Prince William Sound in August 2004.

Area	Month	Prey category and <i>N</i>	2001			2002			2003		
			Small	Large	Signifi- cance level	Small	Large	Signifi- cance level	Small	Large	Signifi- cance level
Prince William Sound	July	Large copepods	4.97	1.15	ns	36.31	27.95	ns	12.70	6.99	ns
		Euphausiids	1.20	0.09	ns	1.84	1.00	ns	0.92	1.46	ns
		Amphipods	20.47	19.74	ns	13.90	4.48	ns	24.29	61.22	<0.001
		Crabs–shrimp	6.72	4.43	ns	3.82	2.25	ns	2.44	7.20	ns
		Pteropods	38.23	46.01	ns	33.79	63.59	<0.001	33.64	12.33	ns
		Larvaceans	18.54	17.70	ns	2.80	0.00	ns	18.27	8.93	ns
		Fish	0.12	1.11	ns	2.62	0.27	ns	4.71	1.39	ns
		<i>N</i>	56	23		46	17		38	13	
	August	Large copepods	2.48	0.71	ns	11.73	2.77	ns	29.77	9.87	ns
		Euphausiids	2.27	3.31	ns	2.11	1.17	ns	8.52	10.15	ns
		Amphipods	77.21	84.93	ns	8.31	8.34	ns	3.63	10.06	ns
		Crabs–shrimp	3.33	2.15	ns	31.95	4.73	<0.01	16.18	33.77	<0.05
		Pteropods	0.07	0.09	ns	41.38	81.71	<0.01	0.07	0.69	ns
		Larvaceans	0.15	0.00	ns	3.05	0.74	ns	30.38	29.81	ns
		Fish	4.98	2.83	ns	0.62	0.54	ns	4.63	4.76	ns
		<i>N</i>	52	16		17	10		26	9	
	July	Large copepods	3.59	11.22	ns	13.66	5.44	ns	8.71	0.63	^a
		Euphausiids	8.85	39.43	<0.01	19.06	19.41	ns	8.99	0.00	ns
		Amphipods	0.79	3.33	ns	2.22	5.96	ns	0.21	0.57	ns
		Crabs–shrimp	0.25	0.00	ns	1.25	0.44	ns	3.33	0.09	ns
		Pteropods	3.68	10.39	ns	34.96	43.57	ns	16.76	16.15	ns
		Larvaceans	68.37	20.30	<0.001	3.65	0.00	ns	46.10	74.92	<0.05
		Fish	0.00	0.00	ns	6.37	5.40	ns	6.96	7.22	ns
		<i>N</i>	24	10		75	26		46	16	
	August	Large copepods	54.01	16.42	<0.001	9.88	3.72	ns	39.18	12.52	<0.001
		Euphausiids	7.49	23.22	<0.05	5.49	1.00	ns	5.04	2.66	ns
		Amphipods	1.33	5.33	ns	8.86	1.35	ns	1.86	1.06	ns
		Crabs–shrimp	7.89	23.12	<0.01	1.50	1.13	ns	3.81	5.59	ns
		Pteropods	11.77	8.60	ns	52.26	77.47	<0.01	16.99	17.56	ns
		Larvaceans	1.25	0.03	ns	7.35	0.00	ns	7.50	15.01	ns
		Fish	2.67	2.01	ns	11.63	15.17	ns	14.27	39.21	<0.01
		<i>N</i>	59	18		54	20		60	22	
Seward Line	July	Large copepods	3.59	11.22	ns	13.66	5.44	ns	8.71	0.63	^a
		Euphausiids	8.85	39.43	<0.01	19.06	19.41	ns	8.99	0.00	ns
		Amphipods	0.79	3.33	ns	2.22	5.96	ns	0.21	0.57	ns
		Crabs–shrimp	0.25	0.00	ns	1.25	0.44	ns	3.33	0.09	ns
		Pteropods	3.68	10.39	ns	34.96	43.57	ns	16.76	16.15	ns
		Larvaceans	68.37	20.30	<0.001	3.65	0.00	ns	46.10	74.92	<0.05
		Fish	0.00	0.00	ns	6.37	5.40	ns	6.96	7.22	ns
		<i>N</i>	24	10		75	26		46	16	
	August	Large copepods	54.01	16.42	<0.001	9.88	3.72	ns	39.18	12.52	<0.001
		Euphausiids	7.49	23.22	<0.05	5.49	1.00	ns	5.04	2.66	ns
		Amphipods	1.33	5.33	ns	8.86	1.35	ns	1.86	1.06	ns
		Crabs–shrimp	7.89	23.12	<0.01	1.50	1.13	ns	3.81	5.59	ns
		Pteropods	11.77	8.60	ns	52.26	77.47	<0.01	16.99	17.56	ns
		Larvaceans	1.25	0.03	ns	7.35	0.00	ns	7.50	15.01	ns
		Fish	2.67	2.01	ns	11.63	15.17	ns	14.27	39.21	<0.01
		<i>N</i>	59	18		54	20		60	22	

^a Result significant but prey category less than 10% of diet.

evenly to a height of 2 mm. The number of grid squares covered (grid counts) and the number of individuals of each prey category were recorded. In stomachs with highly abundant, small prey items, the larger and rarer prey items were removed, and their grid counts and numbers recorded. The remaining portion containing numerous small individuals was subsampled using a Folsom plankton splitter. The number and grid count of these numerous items were determined for the subsample and expanded to the total sample. Prey volumes were not calculated for fish stomachs collected in 1999; instead, the numerical counts in each prey category were multiplied by the estimated weights of individual prey items (as per Boldt and Haldorson 2003). For each fish, prey weights were summed across all prey categories to calculate total prey weight. For the years 2000–2003, prey composition values (by percent volume [%VOL]) were multiplied by total gut content weight (minus estimated mucus and stomach tissue weight) to estimate prey

category weights. In 2004, while volumetric prey composition was measured, actual prey group weights were also recorded to the nearest 0.0001 g using a digital scale. Proportional weights by prey category were averaged and converted to a percentage (%WT).

The methods of diet analysis were the same as those in Armstrong et al. (2005). Diet composition, expressed as a percentage of volume or weight (%VOL or %WT), was used as the primary metric because this was a more relevant measure than prey number when calculating the energetic value of prey to pink salmon.

The proportion by volume of each prey category (p_{if}) was calculated as

$$p_{if} = \frac{v_{if}}{\sum_i v_{if}},$$

where v_{if} indicated the grid count (volume) in the i th prey category for the f th fish.

The proportions in each prey category were averaged

TABLE 1.—Extended.

Area	2004		Signifi- cance level
	Small	Large	
Prince William Sound	18.16	7.82	ns
	5.29	5.77	ns
	15.44	37.02	<0.05
	15.34	20.15	ns
	22.40	10.96	ns
	12.78	16.49	ns
	1.57	0.00	ns
	34	11	
Seward Line	21.93	34.06	ns
	8.10	3.27	ns
	3.54	6.21	ns
	4.32	1.53	ns
	43.20	5.98	<0.001
	6.03	10.90	ns
	11.40	33.38	<0.05
	49	18	
	35.35	33.03	ns
	6.51	33.30	<0.01
	6.24	10.34	ns
	0.98	2.86	ns
	2.34	1.50	ns
	35.32	7.59	<0.05
	6.12	9.58	ns
	36	12	

across all fish at a station (n) to determine the average volumes of prey categories (\bar{p}_i) and converted to percentages according to the formula

$$\bar{p}_i = \frac{\sum p_{if}}{n} \times 100.$$

The average %VOL of each prey category was calculated for each station, area (CGOA or PWS), water mass (PWS, ACC, Front, or Trans), hatchery or wild cohort (AFK, CCH, SGH, WNH, or wild), or fish size-group by area (PWS-large, GAK-large) depending on the analysis. Any prey group with a diet percentage averaging less than 5% (e.g., insects) was included in the “other” category. Fish with empty stomachs were not included in calculation of averages.

The stomach content index (SCI), a measure of gut fullness, was calculated as

$$SCI = \frac{SCWT}{BWT - SCWT} \times 100,$$

where SCWT is stomach content weight (g), BWT is total fish body weight (g), and SCI is expressed as a percentage of BWT. Mean SCI values were used to compare stomach fullness among years, among months within specific areas or water masses, and between hatchery and wild cohorts. Sampling times (hours past dawn) were generally comparable within areas for comparisons among years, months, hatchery cohorts, and fish sizes. Fullness comparisons across habitats could not be analyzed, however, owing to the potential effects of vessel-time sampling anomalies on gut fullness. Because gut fullness progressively increases throughout daylight hours to a peak about 12 h after dawn (Armstrong et al. 2005), the sequence of sampling times among water masses was occasionally confounded.

To compare relative diet quality across temporal or spatial scales or between small and large fish size-groups, the composite energy derived from the diet was calculated. The proportion by weight of each major prey group was multiplied by the energy density of that prey group (values from Davis et al. 1998 and N. Davis, unpublished data, expressed in Joules per gram); the resultant products were summed across all prey groups and averaged for all fish within a test group and termed composite energy density.

Statistical analyses.—Multivariate analysis of variance (MANOVA) tests were used to identify the most important factors with respect to comparisons of fish size, diet composition, gut fullness, and composite diet energy. Subsequent analysis of variance (ANOVA) tests (fixed effects at $P < 0.05$) were used to evaluate variation in diet proportions of key prey. Diet proportions (arcsine square-root transformed; Zar 1984) of each major prey category were compared among years (interannual, August only, GAK stations 1–6 combined), and among year, month, and area between hatchery and wild fish, among hatchery cohorts, among year, month, and area between the largest quartile of fish versus smaller fish, and among years for the largest fish. The ANOVA tests were used to compare diet composition by years (2001–2004), months (July and August), areas (PWS and CGOA [CF, GAK, and West stations combined]), and water masses (PWS, ACC, Front, and Trans) to determine whether there were significant differences. If a significant difference occurred, a posteriori comparisons followed using Scheffé’s test (for unequal sample sizes). Data were analyzed with a standard statistical software SPLUS 2000 (MathSoft 1999). For among-group comparisons, results for those groups of at least 10 fish were reported.

In addition, comparisons of gut fullness (SCI) and fish body size were examined for differences between

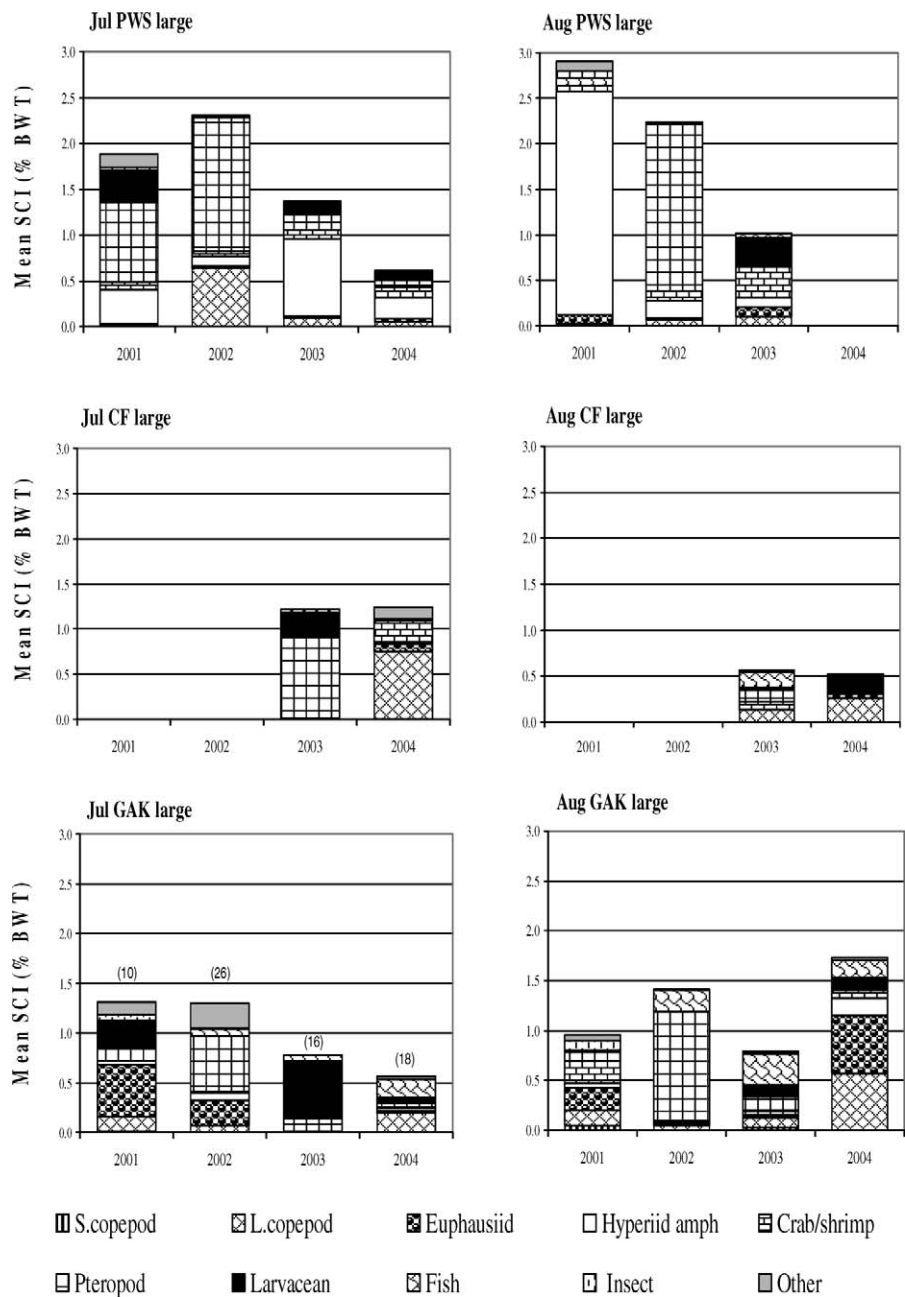


FIGURE 4.—Diet composition by percent volume scaled by gut fullness (mean stomach content index [SCI] expressed as a percentage of body weight [BWT]) for large (fourth-quartile) juvenile pink salmon in Prince William Sound and along the Cape Fairfield Line (CF) and the Seward Line (GAK), July and August 2001–2004.

fish groups in all comparisons (interannual, hatchery and wild, small versus large fish, and for large fish by year and month and habitat) and ANOVA (and Scheffé's test) results were reported. Differences in composite diet energy densities were also examined

using ANOVA tests for the large fish by year and month and for all fish grouped by year, month, area, and habitat.

Interannual analysis.—We hypothesized that diet composition would be related to survival and should

TABLE 2.—Analysis of variance results for the composite energy densities (J/g) of the diets of large juvenile pink salmon by month, year, and sampling area (GAK = Seward Line, PWS = Prince William Sound, CF = Cape Fairfield Line, and WF = west of Seward Line); ns = not significant.

Factor	df	Residuals	F	P-value	Relationship	Critical value of F
July						
Year	3	155	4.0303	<0.01	2003, 2004 > 2001, 2002	2.8265
Area	2	155	20.3966	<0.001	GAKI > PWSI > CFI	
Year × Area	4	155	2.4970	<0.05		
2001	1	30	8.8808	<0.01	GAKI > PWSI	2.0423
2002	1	41	5.7865	<0.05	GAKI > PWSI	2.0195
2003	2	37	14.0523	<0.001	GAKI > PWSI, CFI	2.9285
2004	2	47	7.4539	<0.01	GAKI > PWSI, CFI	2.8995
August						
Year	3	142	8.1247	<0.001	2003 > 2004 > 2001, 2002	2.8293
Area	3	142	5.2365	<0.01	GAKI > PWSI, CFI > WFI	
Year × Area	3	142	0.4480	ns		
2001	1	32	17.4081	<0.001	GAKI > PWSI	2.0369
2002	1	28	3.2141	ns		
2003	3	56	2.3990	ns		
2004	1	26	0.2726	ns		
September^a						
Year	1	42	0.6465	0.4259	ns	2.0181
Area	2	42	1.0995	0.3424	ns	
Year × Area		42		ns		

^a No data collected in 2002 and few fish found in 2004.

vary from year to year, since there were two low-survival years (2001 and 2003), two mid-survival years (1999 and 2000), and two high-survival years (2002 and 2004) included in our study. We compared diet composition, gut fullness, and composite diet quality for all juvenile pink salmon caught on the Seward Line during August for each year from 1999 to 2004.

Hatchery versus wild analysis.—We hypothesized that the diets of hatchery and wild fish would be different, as hatchery fish are conditioned to feed on pellets. To test this hypothesis, we compared diet composition by hatchery cohort versus wild fish during 2001–2004. Otolith-marked fish from each hatchery and unmarked (wild) fish from each sampling area (PWS and CGOA) were grouped, and average body size, diet composition (by %VOL), and gut fullness values were calculated by area for each month (July and August) and year when sample sizes were sufficient.

Diet-size analyses.—We hypothesized that the diets of the large (fourth-quartile size) fish would differ from those of the small fish (first through third quartiles combined). To test this hypothesis, the diet compositions, gut fullness, and composite energy densities of small and large fish were compared among each year–month–area combination. All fish from a year, month, and area were sorted by increasing FL and grouped into quartiles. The mean diet compositions by prey category (expressed as %VOL), mean gut fullness, and mean composite energy densities were calculated for the

small and large fish. Our evidence for size-selective mortality suggests that mortality removes most fish in the three lower size quartiles (Moss et al. 2005; Cross et al. 2008); thus, a comparison of the fourth quartile with the first to third quartiles is relevant to the ecological processes operating on these populations.

In addition, we wanted to examine the differences in diet composition of large (fourth-quartile) fish between high (2002 and 2004) and low (2001 and 2003) survival years. The fastest growing fish are generally considered to have a survival advantage over slower growing fish. The mean diet composition, gut fullness, and composite energy densities of large fish from each year, month, and area were compared across years (2001–2004).

Habitat analysis.—We hypothesized that diet composition would vary by habitat as a result of differences in productivity or prey availability. To test this hypothesis, fish sampled during 2001–2004 were grouped by water mass designation assigned to each station, and diet composition (expressed as %VOL), gut fullness values, and composite diet energy densities were calculated by water mass for each year and each month from July to September and compared across years (2001–2004). Water masses were designated as estuarine (PWS), Alaskan Coastal Current (ACC), front (Front), and transitional to the continental shelf and the Alaskan Stream (Trans) based on salinity measurements and conductivity, temperature, and depth (CTD) profiles recorded at each station. Habitats were defined by

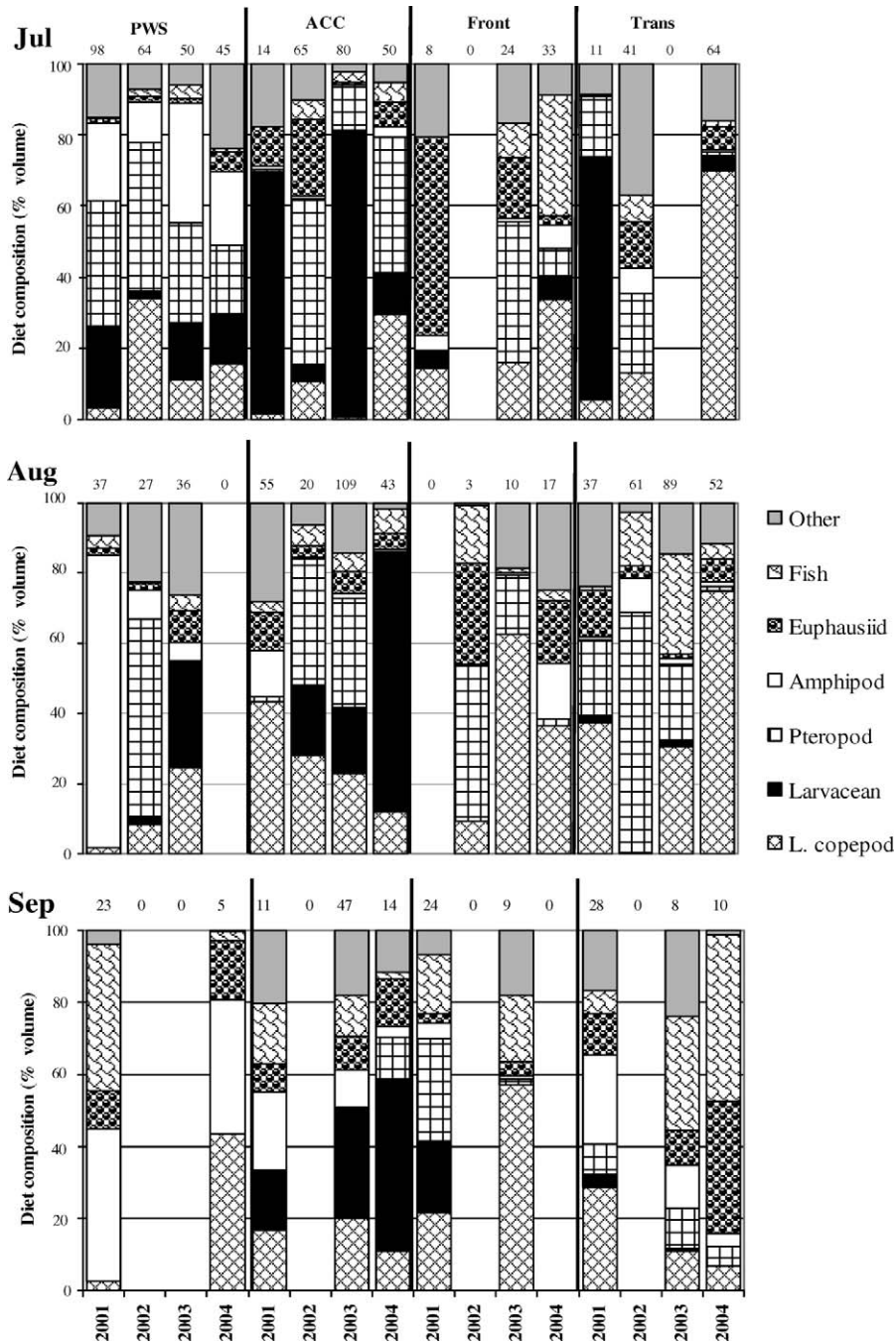


FIGURE 5.—Diet composition of pink salmon by habitat or coastal water mass for all northern coastal Gulf of Alaska locations, July through September 2001–2004. Habitats are designated as the estuarine Prince William Sound (PWS), the Alaska Coastal Current (ACC), the midshelf area (Front), and the outer-shelf area (Trans). Sample sizes are noted above the bars.

salinity values in the upper 5 m as follows: (1) estuarine if the station was sited within PWS, (2) inner shelf (ACC; <30 practical salinity units [psu]), (3) midshelf (Front; ≥ 30 and <31.5 psu), and (4) outer shelf (Trans; >31.5 psu). Some exceptions to these criteria were encountered during July 2003 and July, August, and September 2004 cruises, when salinity values across all CGOA stations were uniformly low and the range of salinities between the ACC and Trans water was compressed. For these cruises, water mass designated as Trans were based on clear breaks in salinity versus depth profiles and the position of the halocline.

Results

Interannual Analysis

During August, juvenile pink salmon diets (by %WT) were less diverse in 1999 and 2000 (when the top three prey categories accounted for 90–95% of the total diet) than in 2001–2004 (when they accounted for 68–79%) (Figure 2). In addition, juvenile pink salmon consumed significantly higher proportions of *Limacina* pteropods in 1999, 2000, and 2002 than in 2001, 2003, and 2004 (ANOVA: $P < 0.001$). Consumption of other prey groups varied significantly among years with no particular pattern, except large copepods comprised a larger fraction of the diets in 2001, 2003, and 2004 than in 2000 and 2002 ($P < 0.001$), and fish comprised a larger fraction in 2002 and 2003 than in 1999–2001 ($P < 0.001$).

Gut fullness (mean SCI; Figure 2) values were significantly higher in 2000 and 2002 (1.6–1.7% BWT) than in 2001, 2003, and 2004 (1.1–1.2% BWT) (ANOVA: $P < 0.001$). The composite energy density of August diets increased steadily from 1999 to 2003 (Figure 2). Gill nets, used in 2000 only, collected fish that were slightly larger (mean FL, 151 mm) than those caught by the trawl nets in 1999 and 2001–2004 (the mean FL ranged from 133 to 139 mm), but there were no significant differences in gut fullness or diet composition attributable to this size difference.

During the years 1999, 2000, and 2002, when pteropods were dominant in August diets and gut fullness values were higher, juvenile hatchery pink salmon experienced mid to high marine survival (5–9%). During the copepod-dominated years 2001, 2003, and 2004, diet quality was in a mid to high range but gut fullness values were consistently lower and marine survival in 2 of 3 years (2001 and 2003) was only 3%. The year 2004 was the anomaly, with low gut fullness and high diet quality values, but high marine survival (8%).

Hatchery versus Wild Analysis

In general, diet composition was similar among all hatchery cohorts and between wild and hatchery fish

within any month–year combination in PWS or the CGOA (Figure 3). Low sample numbers (for individual hatcheries) hampered two of the potential year–month–area group comparisons. In those cases (August–PWS for both 2002 and 2003), we combined all hatchery fish and compared their diets with diets of wild fish for that year–month–area group. There were only two cases among all the comparisons in which significant differences in diets were found. In July 2004, wild fish in PWS consumed more euphausiids than hatchery fish (Figure 3 [all hatcheries combined]; $P < 0.05$), and in July 2002 AFK fish on the Seward Line consumed significantly more large copepods than SGH and WNH fish (Figure 3; $P < 0.001$).

In addition, gut fullness (mean SCI) did not differ significantly between hatchery and wild fish or among fish from different hatcheries during any of the years in PWS (data not shown). There was only one case, July 2002 on the Seward Line, when gut fullness was significantly higher for SGH and WNH than for AFK fish (1.2%, compared with 0.7% BWT, ANOVA: $P < 0.01$). In this case, diet composition also differed significantly (there was a higher proportion of large copepods in diets of AFK fish, whereas *Limacina* pteropods were the primary prey for fish from SGH and WNH). Since diet composition was similar between hatchery groups and wild fish, there was no difference in diet quality (as measured by energy density). The lack of major differences support the premise that hatchery and wild fish generally fed upon similar prey, at similar rates in PWS or the CGOA along the Seward Line within a given month and year.

Diet Comparison between Small (First-to-Third Quartile) and Large (Fourth-Quartile) Fish

Generally, the diets of small and large pink salmon did not differ significantly (Table 1), showing no consistent patterns in prey choice between large and small fish. Gut fullness and diet quality did not differ significantly between small and large fish in PWS in July, except during 2004 when smaller fish exhibited higher gut fullness than the largest fish (1.6 versus 0.6% BWT; $P < 0.05$). On the Seward Line there were significant differences in gut fullness and diet quality between fish of different sizes; however, those differences did not correspond with high and low survival years (data not shown).

Diet of Large (Fourth-Quartile) Fish in High- versus Low-Survival Years

Pteropods dominated the diets of large fish in both July and August in PWS and on the Seward Line in 2002 (Figure 4; note the scaling by gut fullness, which is intended to reflect relative prey category dominance

TABLE 3.—Analysis of variance results for the diet composition (% volume) of juvenile pink salmon by year and water mass (habitat) by month. The years were 2001–2004, the months July–September, and the habitats estuarine (Prince William Sound), Alaska Coastal Current, midshelf (Front), and transition to the outer shelf (Trans). Mean squared error of the residuals are shown in the bottom row for each by month, by species analysis. See Table 4 for relationships; ns = not significant.

		Large copepods		Euphausiids		Amphipods		Pteropods	
Factor	df	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
July									
Year	3	77.12	<0.001	12.2	<0.001	9.8	<0.001	20.27	<0.001
Habitat	3	27.16	<0.001	17.18	<0.001	80.74	<0.001	15.5	<0.001
Habitat	7	16.47	<0.001	13.18	<0.001	7.76	<0.001	9.69	<0.001
× year									
Error		0.1229		0.0636		0.061		0.206	
August									
Year	3	35.09	<0.001	1.07	ns	203.29	<0.001	137.28	<0.001
Habitat	3	20.55	<0.001	1.79	ns	164.68	<0.001	18.25	<0.001
Habitat	7	31.76	<0.001	3.66	<0.001	64.9	<0.001	8.2	<0.001
× year									
Error		0.1502		0.0631		0.0468		0.1171	
September									
Year	2	2.46	ns	9.39	<0.001	23.47	<0.001	8.2	<0.001
Habitat	3	4.08	<0.01	3.75	<0.05	20.65	<0.001	24.98	<0.001
Habitat	4	4.91	<0.001	2.78	<0.05	0.28	ns	4.8	<0.01
× year									
Error		0.1773		0.0711		0.0929		0.0403	

and contribution across years). During July large fish in PWS ate more large copepods in 2002 and on the Seward Line consumed a greater proportion of large copepods and fish in 2004 than during the other 3 years. During August 2001 and 2003 (low-survival years), large fish in PWS ate more hyperiids and larvaceans than during 2002 (high-survival year). The large fish on the Seward Line in August 2004 ate more large copepods than in 2002, and more euphausiids than during 2002 and 2003. During the high-survival years, pteropods in 2002 and large copepods, euphausiids, and fish dominated the diets of large fish in 2004.

Gut fullness analyses showed that large fish in PWS consumed significantly more food in July 2002 than in 2004 (Figure 4; ANOVA: $P < 0.001$) and generally less when hyperiid amphipods comprised a major fraction of the diets. During August 2003 in PWS, fish consumed significantly less food than in 2001 and 2002. On neither the Cape Fairfield Line (CF) nor the Seward Line in August were differences found in gut fullness between years. Composite diet energy densities of large fish were significantly greater in 2003 and 2004 than in 2001 and 2002 and greater for Seward Line fish than for PWS and CF fish in both July and August (Table 2), reinforcing the premise that the earlier juvenile fish could leave PWS in July, the better the diet quality they would encounter in the CGOA.

Habitat Analysis

Diets varied significantly by habitat or water mass across months and years (Figure 5). Diet variation

among water masses was significant (MANOVA: $P < 0.001$) among years, months, areas (PWS or CGOA), and years.

In July, diets within PWS were generally composed of pteropods and large copepods (especially in 2002), larvaceans (in 2001, 2003, and 2004), and hyperiid amphipods. Hyperiid amphipods were significantly more important in PWS across all years compared with other habitats (ANOVA: $P < 0.001$; Tables 3 and 4). Pteropods were more important in PWS and the ACC than in Trans especially during 2002 and 2004. Large copepods were less important in the ACC than in the other habitats, especially PWS in 2002, Front in 2001 and 2003, and Trans in 2004. Larvaceans were more important in the ACC than in PWS in 2001 and 2003 (ANOVA: $P < 0.001$). In the ACC, either larvaceans (in 2001 and 2003, low survival years) or pteropods (2002 and 2004, high survival years) formed the majority of juvenile pink salmon diets during July. Euphausiids were more important in diets at Front in 2001 and 2003 than in PWS or the ACC. In July 2004, fish prey were more important at Front than in other habitats during 2001–2003.

In August in the ACC, Front, and Trans, large copepods (in 2001, 2003, and 2004) or pteropods (in 2002) provided most of the diet. Large copepods were more important in the ACC than in PWS during 2001 and 2002 and at Front and Trans than in the ACC during 2003 and 2004 (ANOVA: $P < 0.001$). Pteropods were the dominant prey in Trans in 2001 and 2002. Hyperiids were more important in PWS

TABLE 3.—Extended.

Factor	Larvaceans		Fish	
	F	P	F	P
July				
Year	127.36	<0.001	8.07	<0.001
Habitat	72.22	<0.001	21.95	<0.001
Habitat	33.72	<0.001	6.35	<0.001
× year				
Error	0.1197		0.0557	
August				
Year	48.35	<0.001	7	<0.001
Habitat	79.47	<0.001	12.07	<0.001
Habitat	34.13	<0.001	6.88	<0.001
× year				
Error	0.0807		0.0901	
September				
Year	15.74	<0.001	0.28	ns
Habitat	12.53	<0.001	4	<0.01
Habitat	3.94	<0.01	4.09	<0.01
× year				
Error	0.1554		0.1732	

during 2001 and larvaceans in the ACC in 2004 than they were in other habitats during all other years. Fish prey was more important in Trans during 2003 and 2004 than in other habitats and other years.

By September, diets were varied and reflected the increase in fish size and ability to capture larval fish (Figure 5). Large copepods and hyperiid amphipods or larvaceans continued to be important diet components.

During July 2001–2004, diet quality (as estimated by the composite energy densities of prey) was significantly lower in PWS than in other water masses (Figure 6, upper panel; Table 5). During July 2004, diets at Front contained greater composite energy density than in the other three habitats. In August for all years combined, the composite energy density was higher in coastal habitats (ACC and Trans) than in PWS (Table 5). Within years, energy density during August was significantly higher in the ACC during 2001 and 2004 and in Trans during 2003 than in other habitats (Figure 6; Table 5). September comparisons were hampered by the lack of a cruise in 2002 and small sample sizes in 2004, but energy density of the diet was higher in Trans in 2004 than in 2001 and 2003 (Figure 6, lower panel).

Discussion

This study has shown that hatchery and wild pink salmon, both during PWS residence and once they initially migrate to the CGOA marine environment, have similar diets and that the correspondence between

higher survival and growth is the result of their being able to exploit specific prey (especially pteropods) during July and August. Juvenile pink salmon often consume a crustacean-based diet of copepods, euphausiids, and larval crab and shrimp (Healey 1991; Landingham et al. 1998; Boldt and Haldorson 2003; Armstrong et al. 2005). Juvenile pink salmon also exploited pteropods (*Limacina*) and larvaceans (*Oikopleura*), both mucus net feeders, which feed on small particles and picoplankton at lower trophic levels (Gorsky et al. 2005). The exploitation of these lower trophic pathways might give pink salmon an advantage over other juvenile salmon and other planktivorous fishes when distributions overlap (Kaeriyama et al. 2000; Ruggerone and Nielsen 2004). The energy densities of large copepods and pteropods are similar (about 2,600 J/g wet weight; Davis et al. 1998; N. Davis, personal communication), although Mazur et al. (2007) found higher values for large copepods at the end of the summer (3,600–5,300 J/g). Higher feeding rates were reported in association with periods when pteropods or larvaceans were the predominant prey for pink salmon, suggesting higher availability of, or selectivity for, these taxa when present (Beauchamp et al. 2007a, 2007b). In addition, there may be different capture and handling costs that make one group a better prey item.

Plankton net surveys indicate that calanoid copepods are the dominant species of zooplankton in the northern CGOA in spring and summer (Coyle and Pinchuk 2003, 2005) but that the abundance of *Limacina* pteropods in the northern CGOA generally increases during the summer and peaks in August (Coyle and Pinchuk 2005). While we are currently unable to provide appropriate zooplankton abundance information to substantiate actual prey availability, we speculate on why pteropods were a desirable prey for juvenile pink salmon. *Limacina* pteropods have a large, dark shell that makes them highly visible, and in some years they occur in highly abundant swarms in the epipelagic zone during daylight hours. In addition, *Limacina* pteropods sequester algal dimethyl-sulfiopropionate (DMSP), the precursor of dimethylsulfide (DMS), which gives them a strong, sulfurous smell (Ackman and Hingley 1965; Levasseur et al. 1994). These attributes probably make pteropod aggregations very easy for salmon to locate and capture.

Moss et al. (2005) determined from back-calculations at specific life history stages that significant size-selective mortality of PWS hatchery pink salmon can occur after the first summer of marine growth. August was defined as the critical period, when the growth rate of juveniles that survived to adulthood increased and diverged from other juveniles. Our results demonstrat-

TABLE 4.—Relationships between factors affecting the diet composition of juvenile pink salmon, by month. Habitat abbreviations are as follows: PWS = Prince William Sound, ACC = Alaska Coastal Current, Front = the mid-shelf area, and Trans = the outer-shelf transition area. Relevant statistics appear in Table 3; ns = not significant.

Factor	Large copepods	Euphausiids	Hyperiid amphipods	Pteropods	Larvaceans	Fish
July						
Year	2004 > 2002 > 2001, 2003	2001, 2002 > 2003, 2004	ns	2002 > 2001, 2003, 2004	2003 > 2001 > 2004 > 2002	2004 > 2002, 2003 > 2001
Habitat	PWS, Front, Trans > ACC	ACC, PWS, Trans > Front	PWS > ACC, Front, Trans	PWS > Trans	ACC > Trans > PWS, Front	Front > PWS, ACC
Habitat × year						
2001	Front > PWS, ACC	Front > PWS, ACC, Trans	PWS > ACC, Trans	PWS, Trans > ACC, Front	ACC, Trans > PWS, Front	ns
2002	PWS > ACC, Trans	ACC, Trans > PWS	PWS, Trans > ACC	PWS, ACC > Trans	^a	ns
2003	PWS, Front > ACC	Front > PWS, ACC	PWS > ACC, Front	PWS, Front > ACC	ACC > PWS, Front	ns
2004	Trans > PWS, ACC, Front	ns	PWS > ACC, Front, Trans	PWS, ACC > Trans	ns	ns
August						
Year	2001, 2003, 2004 > 2002	ns	2001 > 2002, 2003, 2004	2002 > 2003 > 2001, 2004	2004 > 2003 > 2001, 2002	ns
Habitat	ACC, Front, Trans > PWS	ns	PWS > ACC, Front, Trans	Trans > PWS, ACC	ACC > Trans > Front > PWS	Trans > PWS, ACC
Habitat × year						
2001	ACC, Trans > PWS	ACC, Trans > PWS	PWS > ACC, Trans	Trans > PWS, ACC	^a	ns
2002	ACC > PWS > Trans	ns	PWS, Trans > ACC	Trans > ACC	ACC > PWS, Trans	Trans > PWS
2003	Front > Trans > ACC, PWS	ns	^a	ACC, Trans > PWS	PWS, ACC > Front, Trans	Trans > PWS, ACC, Front
2004	Trans > Front > ACC	ns	Front > ACC, Trans	^a	ACC > Front, Trans	ns
September						
Year	ns	ns	2001 > 2003	2003 > 2003	ns	ns
Habitat	ns	ns	PWS > ACC, Front, Trans	Trans, Front > PWS, ACC	ACC > PWS, Trans	Trans > ACC
Habitat × year						
2001	ACC, Front, Trans > PWS	ns	ns	ns	ACC > PWS	PWS > ACC, Front, Trans
2002	No data	No data	No data	No data	No data	No data
2003	Front > ACC	ns	ns	ns	ns	ns
2004	ns	ns	ns	ACC > Trans	ACC > Trans	Trans > ACC

^a Prey category not 10% of diet.

ed interannual variation in two different suites of prey organisms available to juvenile pink salmon in August: one suite dominated by pteropods and one dominated by large copepods, with higher marine survival associated with pteropod-dominated diets. Lower gut fullness levels during 2003 (a low-survival year) and 2004 (a high-survival year) might have resulted from the earlier sampling times. We recognize that sampling time of day can affect gut fullness (Armstrong et al. 2005), but because there did not seem to be any bias in sampling protocols during those 2 years, lower fullness levels probably reflected lower prey abundances, prey patchiness or depletion, greater competition, or some other factor.

The lack of significant differences in diets and gut fullness between hatchery and wild juvenile pink

salmon either in PWS or on the Seward Line indicated that PWS hatchery fish could compete with wild fish for the available food. Boldt and Haldorson (2004) also found that hatchery and wild fish from the same geographic region contained similar energy densities. The carrying capacity of PWS with respect to juvenile pink salmon habitat and the effects of large-scale releases of hatchery fry on wild fry in the northern CGOA are relevant but beyond the scope of this paper (Reisenbichler and Rubin 1999; Hilborn and Eggers 2000; Wertheimer et al. 2001; Chilcote 2003; Nickelson 2003; Morita et al. 2005). Because diets of hatchery and wild pink salmon were similar, we can be relatively certain that future bioenergetic modeling of PWS pink salmon as part of the GLOBEC Synthesis Program will be valid for both wild and hatchery fish.

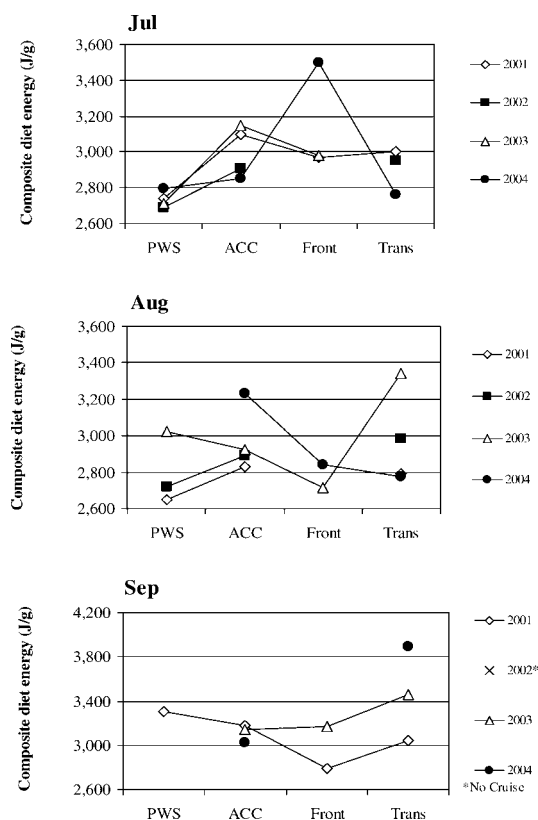


FIGURE 6.—Composite energy density of juvenile pink salmon diets by habitat during July, August, and September 2001–2004. Habitats are as in Figure 5.

The link between diet and survival is growth. Juvenile pink salmon growth in the CGOA was indeed faster during high-survival years than in low-survival years (Moss et al. 2005; Beauchamp et al. 2007b; Cross et al. 2008). Faster growth and attaining a larger size is thought to confer a greater survival advantage upon juvenile pink salmon in freshwater, estuarine, and marine environments (Willette et al. 1999; Beamish and Mahnken 2001; Cross et al. 2005; Moss et al. 2005; Beamish et al. 2006). Many juvenile pink salmon stay within an estuarine environment in July and make the transition to coastal marine waters in August, possibly responding to better feeding opportunities, prey depletion, temperature or salinity cues, or the need to adjust to their increasing body size and changing physiological needs (Orsi et al. 2000; Willette et al. 2001; Beauchamp et al. 2007a). Our results support a strategy in which faster growing fish (fourth quartile) that are able to leave PWS earlier in July take advantage of better feeding opportunities and experience diets of greater quality in the nearshore coastal environment and, thus, might have a better chance of

survival. In 2004, this was even more evident in that the fastest growing fish may have begun to leave PWS and the inner-shelf CGOA by early July, and may have left our study area completely by August (Cross 2006; J. Piccolo, unpublished data).

Pteropod-dominated diets and higher gut fullness in the CGOA during August in 1999, 2000, and 2002 corresponded to higher annual survival rates (5–9%), while in 2001 and 2003 copepod-dominated diets and lower gut fullness corresponded to lower marine survival rates (3%). Fine-scale temporal and spatial diet analyses addressed the earlier month of July and the comparison between PWS and different CGOA water masses.

Diets varied by water mass (habitat) as juveniles moved from the estuarine PWS to progressively more saline habitats in the CGOA, demonstrating that different feeding opportunities were available among years for juvenile pink salmon within these areas (Armstrong et al. 2005). During July in PWS, diets of juveniles contained mostly hyperiid amphipods and pteropods, and gut fullness was generally higher than

TABLE 5.—Analysis of variance results for the composite energy densities (J/g) of juvenile pink salmon diets. See Table 4 for habitat abbreviations; ns = not significant.

Factor	df	Residuals	F	P-value	Relationship	Critical value of F
July						
Year	3	605	0.7035	ns		2.8034
Habitat	3	605	21.9795	<0.001	ACC, Front > PWS, Trans	
Year × habitat	7	605	8.4356	<0.001		
2001	3	104	27.4471	<0.001	ACC, Front, Trans > PWS	2.8418
2002	2	161	9.5299	<0.001	ACC, Trans > PWS	2.8253
2003	2	152	16.1790	<0.001	ACC > PWS	2.8271
2004	3	188	19.7246	<0.001	Front > PWS, ACC, Trans	2.821
August						
Year	3	576	7.087	<0.001	2003 > 2004, 2002 > 2001	2.8038
Habitat	3	576	3.5661	<0.05	ACC, Trans > PWS	
Year × habitat	7	576	8.3112	<0.001		
2001	2	142	4.8125	<0.01	ACC > PWS	2.8293
2002	3	97	2.0444	ns		2.8452
2003	3	228	8.8006	<0.001	Trans > ACC, Front	2.8165
2004	2	109	19.1451	<0.001	ACC > Front, Trans	2.8397
September^a						
Year	2	189	0.4383	ns		2.8208
Habitat	3	189	3.1971	ns		
Year × habitat	4	189	4.0521	<0.01		
2001	3	92	1.522	ns		2.8479
2003	2	71	0.9096	ns		2.8637

^a No data were collected in 2002; no fish were found in PWS in 2003 or in Front in 2004; altogether, too few fish were found in 2004 to analyze.

in the CGOA, but diet quality was low. The diets of fish that migrated to inner-shelf ACC habitat in the CGOA during July were dominated by larvaceans in low-survival years and by pteropods in high-survival years. Diet quality in July in 2001, 2002, and 2003 was lower for fish in PWS than for those in the ACC, Front, and Trans. In August, when fish generally moved to the more productive outer-shelf CGOA (most saline), large copepods and pteropods were dominant prey, and composite diet quality was generally better than in PWS. The increased importance of both euphausiids and larval fish prey in the Front and Trans habitats relative to PWS and the ACC during July and August accounted for much of the difference in higher quality diets. Thus, timing of migration from PWS to the coastal environment is crucial.

Diets in the ACC in July were dominated by larvaceans in low-survival years and by pteropods in high-survival years. Higher feeding rates were associated with periods when higher proportions of pteropods or larvaceans contributed to the diet. Thus, a higher feeding rate, implying greater availability of non-crustacean prey, overcompensated for the reduction in energy density of these prey (Beauchamp et al. 2007a, 2007b). We conclude that spatial variation in diets of juvenile pink salmon in July, as they exit PWS and move to the inner-shelf CGOA, plays a critical role in marine growth and survival.

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